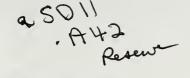# Historic, Archive Document

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Managing Habitats for White-tailed Deer

Black Hills and Bear Lodge Mountains of South Dakota and Wyoming

Carolyn Hull Sieg and Kieth E. Severson

Abstract

The white-tailed deer is one of the most studied animals in North America, yet much of the available information has been derived in ecosystems different from the Black Hills. The Black Hills are unique in that the dominant species, ponderosa pine, has excellent regenerative abilities. This attribute, combined with timber management practices and fire suppression efforts in the last century, has allowed pine to expand at the expense of other plant communities. A critical first step in maintaining viable white-tailed deer populations in the Black Hills is identifying key winter ranges. Given that protein and energy are limiting in winter forages in this region, the emphasis of management on these ranges should be to enhance forage quality and quantity. Prescribed burning and timber harvest can be used to enhance the forage base. Grazing systems designed to remove livestock from these key winter ranges before late summer will provide a greater portion of the woody plants for deer use. Research needs focus on understanding how changes in Black Hills community patterns have influenced deer foraging strategies and habitat use, and on the need for ecologically based techniques to maintain consistent forage quality. Addressing these needs in an ecosystem framework will result in habitat for not only deer, but also for a multitude of other animal and plant species.

Cover photo courtesy of Wyoming Game & Fish Department

Managing Habitats for White-tailed Deer in the Black Hills and Bear Lodge Mountains of South Dakota and Wyoming

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INTRODUCTION

The white-tailed deer is one of the most studied animals in North America. However, most information is from ecosystems quite different from the Black Hills and from non-migratory deer herds. Populations in the Black Hills also use habitat differently. Ponderosa pine is the dominant tree species in the Black Hills, and pine regeneration is excessive in many areas. The flora of the Black Hills is complex, consisting of species from several floristic regions: the Rocky Mountains (30%), Eastern Deciduous Forest (9%), Great Plains (17%), Northern Boreal Forest (6%), Southwestern species (5%), and others (33%) that include exotic plants and species which occur across North America (Van Bruggen 1985).

In this paper, we summarize literature pertaining to:

1. Habitats used by white-tailed deer in the Black Hills and Bear Lodge Mountains of western South Dakota and northeastern Wyoming;

2. Disturbance factors affecting those habitats;

3. Deer habitat requirements (food and cover) in this region; and

4. The interaction of white-tailed deer with other ungulates.

We propose techniques and strategies for managing habitats and then outline research needs for managing white-tailed deer habitat in the Black Hills. Plant nomenclature follows Great Plains Flora Association (1986) (see Appendix 1; Appendix 2 contains animal nomenclature).

GEOGRAPHIC SETTING AND CLIMATE

The Black Hills and associated Bear Lodge Mountains are an isolated extension of the Rocky Mountains, stretching 118 mi (190 km) north to south and 60 mi (95 km) east to west. Elevations range from approximately 3,002 ft (915 m) to 7,241 ft (2,207 m). The majority of the land in the Black Hills and Bear Lodge Mountains is managed by the Federal government.

The Black Hills are divided into four distinct physiographic areas:

1. The Central Crystalline Area;

2. The Limestone Plateau;

3. The Red Valley; and

4. The Dakota Hogback (Darton and Paige 1925).

The Central Crystalline Area is the result of granitic uplift; it is mostly comprised of granites, schists, and slate. The Limestone Plateau surrounds the Central Core and is a relatively level sedimentary formation. The Red Valley is also sedimentary in origin, and includes siltstones and shales. The Dakota Hogback encircles the Red Valley; it consists of interbedded sandstone and shale. Major creeks in the Black Hills include Inyan Kara, Sand, Spearfish, Whitewood, Elk, Box elder, Rapid, Spring, Battle, French, Beaver, and Fall River. All surface flow eventually drains into the Cheyenne River.

With the exception of the Red Valley region and the prairie inclusions, most soils in the Black Hills developed under the influence of trees. Alfisols, or what were previously called Gray Wooded soils, predominate at higher elevations and are common in ponderosa pine forests. Radeke and Westin (1963) described a typical Alfisol as having a thin, organic-rich A horizon, 3-15 in (7.6-38.1 cm) thick, under which laid a thin (2-9 in; 5.1-22.9 cm) relatively leached B/E horizon on top of a clay-enriched Bt horizon. The largest expanses of Mollisols, or prairie soils, are found in Slate, Reynolds, and Gillette Prairies and in bottomlands in the Black Hills. These soils are characterized by a thick mollic (dark and enriched with organic matter) epipedon (surface layer). Entisols and Inceptisols, or shallow, relatively young soils are more common on steep slopes where less moisture enters the soil and erosion rates are high (Sieg 1993).

Average annual precipitation in the Black Hills ranges from approximately 18 in (46 cm) to 26 in (66 cm) (Orr 1959). Approximately 60 to 70% of the total precipitation occurs between May and October. Thunderstorms bring a large portion of summertime precipitation and may be accompanied by gusty surface winds, lightning, hail, and heavy rainfall (Miller 1986). Seasonal and

yearly droughts are common. Mean temperatures of the Black Hills generally are higher in the winter and lower in the summer than on the surrounding Great Plains. Winters can range from very mild, with little or no snow and thawing daily temperatures, to severe, with complete snow cover and subzero temperatures for a month or more at a time. Severe spring blizzards occur on the average of every three to four years (Miller 1986).

BLACK HILLS HABITATS

Ponderosa pine dominates approximately 70% of the land area in the Black Hills and Bear Lodge Mountains (Thilenius 1972). Quaking aspen, paper birch, and Black Hills or white spruce are common in localized areas at higher elevations. Other important vegetation types include mountain mahogany chaparral in the southern portion of the Black Hills, bur oak belt on the northern and eastern fringes, and riparian communities. Reynolds, Slate, and Gillette Prairies and the Bald Hills are unique grassland types in the central Black Hills; smaller meadows are scattered throughout the area.

Ponderosa Pine

Ponderosa pine in the Black Hills produces relatively dependable seed crops; coupled with favorable spring and summer moisture conditions, pine reproduction is excellent (Boldt and Van Deusen 1974). High pine densities are common in most naturally regenerated stands, and crowded stands may remain dense for their lifespans.

Thilenius (1972) examined vegetation, soil, and site characteristics of 100 ponderosa pine stands in the Black Hills and produced a classification of the forest into 13 habitat units of which the ponderosa pine/common juniper/white coralberry/Oregon grape was the most common. Hoffman and Alexander (1987) subjectively classified 68 ponderosa pine stands based on their "potential" (or "climax") vegetation in the absence of disturbance. The ponderosa pine/white coralberry habitat type was the most common of the seven ponderosa pine types they identified.

Quaking Aspen/Paper Birch

Aspen occupies about 5% of the total land area in the Black Hills and Bear Lodge Mountains (Severson and Thilenius 1976). McIntosh (1949) observed that stands dominated by quaking aspen and paper birch were common in the northern Black Hills, especially on north-facing slopes where pine had been cut or burned.

Severson and Thilenius (1976) classified aspen stands of the Black Hills into nine groups based on criteria similar to those used by Thilenius (1972). The most important group was characterized by a high average density of small aspen. Most stands in this group had burned less than 40 years previously and had an understory dominated by wild spirea and yellow vetchling.

Most aspen stands in the Black Hills revert to pine- or spruce-dominated communities in the absence of fire. However, Severson and Thilenius (1976) identified two climax aspen types, both of which had understories dominated by either beaked hazelnut or ironwood. Hoffman and Alexander (1987) also identified one climax aspen habitat type in the Black Hills: quaking aspen/beaked hazelnut. Paper birch and bur oak were often present in the overstory.

Bur Oak

Bur oak reaches its western range limit in western North and South Dakota and northeastern Wyoming. Its distribution in the Black Hills coincides with primary white-tailed deer winter range (Severson and Kranz 1978). Bur oak assumes a variety of growth forms in the Black Hills, ranging from a shrub under pine canopies at higher elevations to large trees on favored sites along streams at lower elevations. McIntosh (1949) described an eastern chaparral subclimax community in the northern Black Hills, where bur oak dominated. Other common woody plants included beaked hazelnut, currants, and a variety of other shrubs. He also described a "deciduous forest post climax," where in the northern portions of the Black Hills, bur oak becomes the dominant tree. Woody subdominants include paper birch and ironwood. McIntosh (1949) also noted the abundance of bur oak, aspen, paper birch, beaked hazelnut, western wild rose, Saskatoon serviceberry, and chokecherry on an area burned by a forest fire 30 years previously in the Tinton area. Thilenius (1972) described four habitat units containing bur oak intermixed with ponderosa pine. Hoffman and Alexander (1987) recognized two bur oak habitat types: bur oak/ironwood and bur oak/snowberry.

Black Hills Spruce

Black Hills or white spruce occurs at high elevations and on cooler slopes and canyon bottoms. McIntosh (1949) recognized a Boreal forest association dominated by Black Hills spruce. Hoffman and Alexander (1987) sampled 10 spruce-dominated stands between 5,699 and 6,693 ft (1,737 to 2,040 m), and recognized two habitat types: Black Hills spruce/twinflower and Black Hills

spruce/grouseberry. They hypothesized that spruce forests in the Black Hills served as summer-fall deer habitat and suggested that spruce stands were important in providing thermal and hiding cover.

Mountain Mahogany

Hoffman and Alexander (1987) described a mountain mahogany/sideoats grama habitat type at low elevations on xeric sites around the southern one-third of the Black Hills. In addition to mountain mahogany, fragrant sumac commonly occurs in this habitat type. Mountain mahogany may also increase in ponderosa pine/ninebark habitats following fires (Hoffman and Alexander 1987).

Riparian and Riparian-Like Areas

In the 1940's, willows, birches and cottonwoods were the most conspicuous riparian species in the Black Hills (McIntosh 1949). A dense shrub zone consisting of a mixture of several willow species including beaked willow, yellow willow, sandbar willow, water birch, and red osier occurs in relatively undisturbed areas at medium to high elevations (Froiland 1990). Froiland (1962) identified 20 species and varieties of willows in the Black Hills; nine were abundant and widely distributed, three species were moderately abundant, and eight were classified as rare. Along small streamsides at upper elevations riparian vegetation was dominated by Black Hills spruce, aspen, and/or paper birch (McIntosh 1949).

McIntosh (1949) described a "deciduous forest post climax," composed of green ash, American elm, boxelder, and hackberry. In the northern and eastern fringes of the Black Hills, bur oak becomes an important component of this association. Sieg (1991) identified three bur oak types. Bur oak was the dominant tree on all three types; green ash and boxelder were co-dominants on floodplains.

The importance of riparian zones as white-tailed deer habitat in the Black Hills is not well documented. In other areas, riparian zones provide food, cover, water, and travel corridors (e.g., Omhart and Anderson 1986). Riparian zones usually constitute an important component of white-tailed deer winter range in the Rocky Mountains (Peek 1984). In eastern Montana, white-tailed deer were observed more often in riparian areas than in ponderosa pine stands or sagebrush grasslands, even though riparian stands occupied only 14% of the land area in the study area (MacCracken and Uresk 1984).

Grasslands and Meadows

McIntosh (1949) recognized mixed-grass, shortgrass, and bunchgrass grasslands in the Black Hills. He noted that mixed-grass prairies surrounded the Black Hills, extended into the pine savannah of the foothills, and dominated as an edaphic climax in larger park-like areas such as Reynolds Prairie. Common species in this type included Junegrass, needle-and-thread, green needlegrass, and western wheatgrass. The shortgrasses, buffalograss, and blue grama dominated heavily grazed sites. The bunchgrass association occurred in the Red Valley and extended into the foothills and was dominated by big bluestem and little bluestem. Pase and Thilenius (1968) identified two kinds of grasslands in the Black Hills: a moist type dominated by Kentucky bluegrass and a dry type corresponding to McIntosh's mixed-grass type.

HISTORICAL DISTURBANCES AFFECTING HABITATS

The forest is a dynamic environment and constant change has occurred both before and since the period of non-native settlement of the Black Hills (U.S.D.A. Forest Service 1994). Most biotic communities in the Black Hills evolved under a regimen of irregular but generally constant change induced by a variety of natural disturbances. In addition to weather, fire was one of the most ubiquitous of these disturbances; but periodic insect and disease outbreaks were also influential. Of lesser importance was the impact of grazing and browsing by native ungulates and dam construction by beavers. Non-native settlers, whose influx began with mining activities in the late 1870's, altered these disturbance patterns and changed the Black Hills biotic communities.

Comparing photographs taken in 1874 during Custer's expedition to the Black Hills with those taken nearly a century later (Progulske 1974, Progulske and Shideler 1984) shows increases in pine tree density, invasion of meadows by pines, and deterioration of riparian habitat along some streams (Hoffman and Alexander 1987). It appears that the Black Hills now supports fewer old-aspen stands and less bur oak than Custer and his compatriots observed. Several exotic plant species occur now, including plants brought in for seeding projects and inadvertently introduced noxious weeds.

Weather

As discussed above, the continental climate of the Black Hills results in high variability in temperature,

precipitation, winds, and humidity. This variable climate influences plant growth both directly and indirectly. Adequate spring and summer rainfall is the most important factor influencing forage supplies in the Black Hills. If rainfall during spring and summer is below normal, forage production will decline (Uresk and Severson 1989). Further, droughts, high temperatures, and desiccating winds increase the likelihood of fires. Some of the largest wildfires in the Black Hills occurred during dry years, such as the Rochford burn in 1931 and the McVey burn in 1939. Precipitation in these years was 9.3 in (23.6 cm) and 11.0 in (27.9 cm), respectively (Miller 1986). Several large wildfires occurred more recently during a three-year drought period, 1987-1989, when precipitation ranged from 10.9 to 13.6 in (27.7 to 34.6 cm).

Other weather influences that affect Black Hills habitats include extreme temperature changes, tornadoes, heavy snows, and floods. For example, in January 1943 a "chinook" caused temperatures to fluctuate as much as 85 degrees, damaging trees over a 50 square mile (129 square km) area (U.S.D.A. Forest Service 1948). An average of two tornadoes occur per year within 100 mi (161 km) of Rapid City (Miller 1986) and have been responsible for breaking small tracts of trees. Heavy snows were responsible for high timber losses in 1933 (U.S.D.A. Forest Service 1948). Flooding influences riparian vegetation and was historically more common than today. Before the construction of Pactola dam on Rapid Creek, floods occurred on the average of every two to three years (Miller 1986). All of these factors, combined, tend to create series of both temporal and spacial habitat patterns in the Black Hills.

Fire

Although few quantitative data are available on historic fire frequency in the Black Hills area, fires were an important ecological force in this region. The increase in pine coverage today compared to that documented by the Custer Expedition photographs (Progulske 1974, Progulske and Shideler 1984) is due, in part, to fire suppression efforts over the last century.

Fisher et al. (1987), working in the Devils Tower region northwest of the Black Hills, determined that tree densities have increased over the last 100 years and that pines have invaded grasslands and increased their densities in savannas. They also found that before 1770 the mean period between fires was 27 years; from 1770 to 1900 the fire return period was 14 years, and since 1900 fires burned on the average of every 42 years.

Historically, fires were started by lightning and American Indians. Lightning strikes in ponderosa pine stands in northwestern South Dakota are most common in July and August, although they occur in every month between April and September (Higgins 1984). Severe thunderstorms are most common in the Black Hills in the summer months (Orr 1959), and journals of early explorers to the region noted the high incidence of lightning scars on ponderosa pine trees. Newton and Jenny (1880) reported that of 100 trees in a small park, 14 had been struck by lightning, some of them more than once. Dodge (1965) made continual notes of the evidence of fire as his expedition in 1875 traveled through the Black Hills.

Higgins' (1986) survey of historical literature indicates that American Indians set fires in nearly every month of the year on the Great Plains; however, April, September and October were peak months for burning. The decrease in time between fires in the Devils Tower region from 1770 to 1900 noted by Fisher et al. (1987) was attributed to the fire setting activities of the Lakotas, who moved into the region around 1765. The consequence of frequent fires set either by lightning or American Indians was a landscape different from today's (Wright and Bailey 1982, Covington and Moore 1992).

These historical fires thinned ponderosa pine stands, eliminated young pines, and in some areas, kept stands open and park-like, with an understory of shrubs and forbs (Wright and Bailey 1982). This type of regeneration in ponderosa pine forest resulted in a forest that was represented by many age classes arranged in distinct groups (Biswell 1989). Thus, a pattern of disjunct groups or clusters or even-aged and even-sized trees, saplings, or seedlings existed, often less than 1 acre (0.4 ha) in size (Wright and Bailey 1982). As surface fires helped to kill the younger, weaker trees and dense thickets in a young pine stand, competition and stand stagnation were minimized, and nutrients in the litter were recycled.

Human interference with the natural fire cycle threatens the existence of quaking aspen in many parts of the country (Wright and Bailey 1982). Many aspen stands in the western United States are in excess of 60 years old (DeByle 1984). Also, as discussed earlier, aspen stands in the Black Hills often are invaded by ponderosa pine. Harmon (1971) cited decadent, overmature aspen stands as contributing factors in the decline of white-tailed deer populations in Minnesota.

Bur oak is another example of a deciduous species that evolved with periodic burning and tolerates fire well. Bur oak trees sprout vigorously following burning (Johnson 1990), although this sprouting response often declines with age (Kramer and Kozlowski 1979). Young bur oak trees have relatively thin bark and are more vigorous; larger bur oak trees are more resistant to injury by fire due to their thick bark (Fowells 1965). Many other woody species in the Black Hills, including chokecherry, snowberry, and willow, sprout vigorously following burning (Wright and Bailey 1982).

Riparian and riparian-like communities in the Black Hills also burned, but at a less frequent interval. These stands tend to be green throughout most of the growing season, have higher relative humidities than uplands, and often have running water or moist soils that would slow the spread of fire into these communities. Therefore, in most years, wildfires would tend to skip over or only burn lightly through these areas (Severson and Boldt 1978). However, the relatively high frequency of fires in adjacent pine and grassland communities would suggest that riparian and riparian-like areas did occasionally burn, especially on hot and windy days during droughty spells.

Insects and Diseases

A variety of insects and diseases have played a role in the ecology of Black Hills communities. One of the more obvious insects, and one that greatly influences the structure of ponderosa pine forests, is the mountain pine beetle. Graves (1899) noted numerous patches of dead and dying timber on the Limestone Plateau that he attributed to the impacts of "bark borers." He described the patches as being rectangular in shape and following the tops of the ridges or running length-wise up and down the slope. In his survey of the Black Hills, he estimated about 3,000 acres (1,214 ha) of trees were killed by these insects. Hopkins (1905) verified that the tree mortality Graves observed was due to mountain pine beetles. Although the 1895 outbreak was the first documented in the Black Hills, other epidemics have occurred since the turn of the century (Schmid and Amman 1992).

Mountain pine beetles can help maintain vigorous growth by removing stagnated, diseased, and injured trees and in recycling dead woody tissue (Wood 1982). Epidemics of pine beetles can kill over 90% of a stand; mortality of this magnitude can change stand structure, species composition, and successional trends (Schmid and Amman 1992). Epidemics of lesser magnitude kill only 10-20% of a stand. Mountain pine beetles also kill relatively more large diameter trees than small diameter trees (Schmid and Amman 1992).

Habitat Requirements of White-Tailed Deer

White-tailed deer use of Black Hills habitats is governed by the deer's requirements, which vary throughout the year. Principal requirements center around their need for adequate quality and quantity of food and adequate cover for security and protection from weather. The habitats described earlier offer different combinations of food and cover and vary in their value as deer habitat depending on spacial and temporal arrangements among habitats.

Foods, Nutrition, and Forage Production

Food habits. Hill (1946) examined stomach contents of 319 white-tailed deer killed in the northern Black Hills and compared percentages of major dietary species with their amounts observed in the field. Preference ratings were calculated as a ratio of percentage in the diet to percentage available in the field. Plant species with high palatability ratings in winter (October-March) included bearberry, Oregon grape, snowberry, and fragrant sumac. Highly palatable species in spring diets included grasses (mainly Kentucky bluegrass), aspen when it leafed out, new rose growth, wild spirea, serviceberry, and chokecherry. Palatable summer species included a variety of forbs and willows, snowberry, and rose hips.

Schneeweis et al. (1972) also studied food habits of white-tailed deer in the northern Black Hills by measuring utilization in deer enclosures and by analyzing rumen contents. Oregon grape was the most important food item during the fall and winter. However, because of its low growth form, its availability decreased with increasing snow depth. During periods of heavy snow cover, common juniper replaced Oregon grape as the most important species. Bearberry was also highly preferred and important during periods of little or no snow cover. Ponderosa pine, lichens, and bur oak were eaten in moderate amounts but were of secondary importance as winter food items. Rumen content analyses from deer collected during summer in aspen stands showed yellow vetchling, Saskatoon serviceberry, and wild spirea were important food items.

Schenck et al. (1972) studied deer diets in the southern Hills. The most important fall foods in the rumens of 52 deer were bearberry, grasses, Oregon grape, western snowberry, and forbs. The most important winter foods in the diet of 64 deer were ponderosa pine, mountain mahogany, and common juniper. Other important winter foods were bearberry, western snowberry, Rocky Mountain juniper, forbs, and grasses. The most important summer foods in rumen samples of nine deer were alfalfa, clover, grasses, and forbs.

One particular concern is the amount of ponderosa pine needles that occur in the diet. Hill (1946) and Hill and Harris (1943) found ponderosa pine to be used slightly to moderately from October through March, but used extensively from April through June. Schneeweis et al. (1972) and Schenck et al. (1972) determined pine to be moderately important and important in winter diets, respectively.

Differences in the amounts of pine in deer diets may be attributable to the time of winter the above studies were conducted. White-tailed deer foraging is dynamic; deer tend to be very selective feeders in early winter but gradually become generalists as the season progresses

and forage is depleted (Brown and Doucet 1991). The increased utilization of pine as winter progressed, as reported by Hill (1946), may result from the gradual elimination of more preferred forage items. Long-term changes in deer diets, such as increased use of pine needles, could also be the result of loss of preferred winter range. Human development on foothills winter ranges has likely forced deer to feed in lower elevation pine-dominated habitats rather than in the more open foothill ranges.

Extensive use of pine needles for food, especially in late winter or spring, may result in increased fawn mortality, directly and indirectly. However, there is no published information on whether or not ponderosa pine needles cause premature parturition in deer. In fact, anecdotal reports have suggested that pine needles have no toxic or abortifacient effects on deer (see review by James et al. 1989).

Nutritional Relationships

Forage is a key component of white-tailed deer habitat during the entire year. Winter forage, whose availability is controlled by duration and severity of weather, has been considered the primary factor limiting cervid populations in the West (e.g., Wallmo et al. 1977) and, consequently, more information is available on the nutritional quality of forages during this season. However, food quality and abundance on summer and fall ranges is also critical. Lactating females, weaned fawns, and mature males after breeding require a nutritious diet to enable them to store adequate subcutaneous fat for the upcoming winter (Mautz 1978). White-tailed deer have evolved adaptations that enable them to survive winters (see review by Verme and Ullrey 1984). They accumulate deposits of subcutaneous fat during late summer and fall, change to an efficient insulative winter coat, feed more during warmer daylight hours, and seek shelter under dense conifers. Further, their food intake decreases regardless of supply and their metabolic rate decreases until, by midwinter, they are in a relatively torpid state. The efficacy of these adaptations depends on the amount of subcutaneous fat the animal was able to store before winter. Although winter range should continue to receive attention, improvement of summer and transitional ranges should also be emphasized in management plans. Managers should strive to provide an adequate amount of forage, in mass and diversity, and to ensure that quality of forage is sufficient each season (Dietz 1972, Wallmo et al. 1977).

A very gradual but steady decline in nutritional levels of the overall forage base (which could be caused by a reduction in number of forage species, a change in species composition, or an overall reduction in forage production) could be caused by several factors. Those that influence nutritional levels in the forage base for white-tailed deer in the Black Hills include natural succession, overuse of forage by wildlife and livestock, increased tree cover, absence of fire, and drought. Effects on deer populations would be equally gradual; a steady but annually irregular reduction in the number of fawns reaching productive age classes would, over time, become more and more critical.

The most obvious effect of malnutrition is starvation, which is easy to predict and observe among cervids. Many populations are more adversely affected indirectly by malnutrition. The effects are more insidious and act through vectors such as an increased incidence of parasitism and disease, an increased susceptibility to predation, an increase in resorption of fetuses and/or stillborn fawns, a lower conception rate, and impairment of rumen functions (which accentuate the problem) (Dietz and Nagy 1976). These effects are not obvious and are difficult to separate from other environmental factors.

Recent studies indicate that effects of malnutrition are not restricted to the current year or even the current generation. Nutritional deprivation of maternal and grandmaternal white-tailed deer has been implicated in survival and mass of first and second generation offspring (Mech et al. 1991). In this case, first and second generation offspring with poorly nourished ancestors were more vulnerable to wolf predation.

Winter Forages

Protein requirements for maintenance have been estimated to be 11% of the daily intake for yearling white-tailed deer and 6 to 10% for adults (Verme and Ullrey 1984). However, forages should be assessed for their dry matter digestibility. Many of the primary species consumed by deer on Black Hills winter ranges (Schneeweis et al. 1972, Schenck et al. 1972) have crude protein contents below these limits. Of the seven species analyzed by Dietz (1972) only fringed sagebrush (7.6%), chokecherry (9.2%), and Saskatoon serviceberry (7.0%) had crude protein contents equal to or greater than the amount needed. The digestible protein contributed by these species would be somewhat less.

Ponderosa pine needles are relatively abundant and available on winter ranges. Reported protein content of pine needles ranges from only 5.2%[2] early in the growing season in the Black Hills to 6.9% at an unspecified time from two sites in Wyoming (Panter and James

[2] Nutritional attributes not followed by a specific reference are on file at the Rocky Mountain Forest and Range Experiment Station, School of Mines Campus, Rapid City, SD, 57701.

1987). Bur oak buds and twigs also contained low levels of crude protein during winter—5.5 and 4.4%, respectively (Severson and Kranz 1978). Bearberry, another abundant winter forage that is often unavailable on winter range because of its low growth form, contained from 5.1 to 5.8% crude protein (Severson and Uresk 1988). Limited information on Oregon grape, another common but low growing species, indicates a high protein content in early summer (10.4 to 12.4%), but winter levels would be lower.

Tannin contents in white-tailed deer forages may impede digestion. While the apparent digestibility of protein is reduced in white-tailed deer consuming tanniferous forages (Robbins et al. 1987a), digestion of the plant cell wall is not reduced beyond that predicted from its content of lignin, cutin, and silica (Robbins et al. 1987b). Salivary proteins that preferentially bind tannins have been identified in mule deer; these proteins reduced absorption of hydrolyzable tannins and potential for tannin toxicity (Austin et al. 1989).

Calcium requirements for growth and antler development are about 0.45% (Verme and Ullrey 1984). Calcium supplies were usually adequate in shrubs (0.69% to 2.3%), but ponderosa pine needles contained only 0.34% (Panter and James 1987). Phosphorus requirements do not exceed 0.28% and may be lower (Verme and Ullrey 1984). Phosphorus levels in Black Hills forages indicate borderline deficiency during the dormant season; most primary forage species have contents that range from 0.09% to 0.18% (Dietz 1972, Severson and Kranz 1978, Panter and James 1987).

Digestible dry matter determined in vitro is a general estimator of available energy and nutrient availability. Digestible dry matter ranging from 50% to 60% was considered excellent for deer in Arizona (Urness 1973). Fringed sagebrush and aspen in the Black Hills had the highest dry matter digestibilities during the winter—57% and 60%, respectively; chokecherry averaged 51%. Western snowberry (41%) had a digestible dry matter content in the intermediate range (Dietz 1972). Digestibility of bur oak buds and twigs was 37% and 31%, respectively (Severson and Kranz 1978); ponderosa pine needles collected in Wyoming ranged from 30 to 42% (Panter and James 1987).

Dietz (1972) and Wallmo et al. (1977) concluded that evaluation of winter ranges is best determined by quantification of nutrients rather than gross availability of forage. Dietz (1972) illustrated this by examining the nutritive characteristics of the most common species in deer winter diets and then related these to the amount of each species present on winter range and to the animals' daily consumption rate. For example, dry matter production of western wild rose was the highest of all shrub species with 25.5 lb/acre (28.6 kg/ha), but it yielded less crude protein (1.5 lb/acre; 1.7 kg/ha) than

fringed sagebrush—2.2 lb/acre (2.5 kg/ha)—which had a dry matter production of 23.7 lb/acre (26.6 kg/ha). Chokecherry production was 4.0 lb/acre (4.5 kg/ha) and yielded 0.3 lb/acre (0.4 kg/ha) of crude protein. He predicted the maximum deer range carrying capacity, based on production of crude protein, to be 20.3 deer days/acre (50.2 deer days/ha). Carrying capacities based on dry matter production, digestible dry matter, and gross energy were predicted to be 20.6, 22.4, and 28.8 deer days/acre (50.9, 55.4 and 71.2 deer days/ha, respectively). Dietz thus concluded that crude protein was the primary limiting factor on Black Hills deer winter ranges. Wallmo et al. (1977), in a similar exercise, concluded that energy was the limiting factor on Colorado mule deer winter ranges.

Summer Forages

Most studies on white-tailed deer nutrition have focused on non-migratory herds. White-tailed deer in the Black Hills are primarily migratory, however, and occupy different ranges in summer and winter. In such situations, summer ranges receive less attention because forage condition and availability generally exceed that on winter ranges. Further, losses on winter range are often dramatic (i.e., starvation) while poor condition summer range is reflected in lower productivity and is thus a more gradual cause of population decline. Julander et al. (1961) and Pederson and Harper (1978) documented notable differences in doe/fawn ratios and percentage of does with twins on good vs. poor condition summer range for migratory mule deer in Utah.

White-tailed deer highly prefer forbs during summer, as previously discussed. Minimum requirements for lactation and for growth of fawns after weaning ranges from 14 to 22% crude protein (Verme and Ullrey 1984); therefore, the importance of forbs cannot be overemphasized. Crude protein contents of 16 to 28% are not uncommon among forbs but these levels drop by half or more as fruits mature. Common dandelion leaves, for example, contained from 20.8 to 28.2% crude protein before flowering and 10.6 to 14.8% after flowering. Forbs analyzed by Severson (1982) contained more crude protein than grasses or shrubs in August collections; composite samples of forbs from aspen understory contained from 8.3 to 10.0% compared to 7.5 to 8.3% for shrubs and 6.1 to 7.5% for grasses.

Deer prefer legumes such as yellow vetchling (Schneeweis et al. 1972). Vetchling was unique in that it produced relatively consistent and significant amounts of forage in thinned stands of ponderosa pine and under aspen regardless of the amount of overstory (Severson 1982, Uresk and Severson 1989). Further, crude protein content of this species did not drop below levels recom-

mended for growing fawns but remained above 14% in August, after flowering occurred (Severson 1982, Severson and Uresk 1988). However, an assessment of digestible protein is necessary to evaluate forage quality.

Phosphorus may be insufficient on summer ranges dominated by aspen. Jelinski and Fisher (1991) noted that calcium:phosphorus ratios greater than 7:1 and 10:1 may be high enough to reduce availability of digestible phosphorus to herbivores. Ratios in yellow vetchling equalled or exceeded these levels (10:1 to 11:1); those in forb composites were 5.5:1, shrub composites 4.4:1, and grass composites 2.2:1 (Severson 1982). Optimum ratios range from 2:1 to 1:2 (McDowell 1992).

Generally, the abundance and diversity of forage plants during the summer provides deer the opportunity for a feeding strategy that optimizes a nutritionally balanced diet (Westoby 1974). Ruminants, like deer, have evolved an ability to select a mix of forages to satisfy nutritional requirements (see review by Provenza 1995); hence forage diversity is essential to nutritional optimization of their diets (Vangilder et al. 1982). White-tailed deer in the Black Hills select plants higher in crude protein and phosphorus, such as yellow vetchling, wild spirea, and western wild rose, compared to plants that were more available during summer (Schneeweis et al. 1982). A land manager's primary task on white-tailed deer summer range would be to maximize diversity of the forage available to the animals.

Although most nutritional requirements are expressed as minimum daily amounts, Dean (1976) suggested that seasonal requirements should be emphasized for wild animals. Nutrient intake should be sufficient to allow young to survive the winter and females to reproduce successfully; whether or not animals receive maintenance rations each day is of secondary importance. In other words, animals on good condition winter ranges can be expected to survive short-term stress periods (e.g., a winter storm) on a low condition diet.

Fall Forages

Stored fat is essential to deer survival in winter; therefore, an abundance of high quality forages on late summer and fall ranges ensures deer are in better condition to survive winter (Mautz 1978). The nutritive value of most herbaceous forage declines precipitously as plants mature and the decline continues, less abruptly, into the winter. Behaviors that expend high levels of energy and interfere with foraging, such as breeding and avoidance of hunters, hinder fat deposition during this period.

It is during this time of the year that woody portions of shrubs, especially terminal ends of twigs, provide relatively higher dormant season levels of protein, phosphorus, and carotene than do forbs or grasses (Welch 1988). This can be partially attributed to translocation of nitrogen and minerals from leaves back into the stem prior to abscission—an adaptation to prevent shrubs from losing nutrients through leaf fall (Dietz 1972).

Most of the shrub forages that are reportedly important on Black Hills fall ranges (e.g., Oregon grape, common juniper, bearberry, ponderosa pine, bur oak, snowberry, and grasses; see Food Habits section) are those that are relatively abundant but are either nutritionally lacking or become unavailable in deep snow. Pine, oak, and the grasses have nutritional limitations as previously discussed. Oregon grape and bearberry are low growing and become unavailable with increasing snow depth. Further, tall shrubs are not common on some fall ranges. In the central Black Hills, tall, nutritious shrubs such as chokecherry, serviceberry, rose, and young aspen were found only in isolated patches (Uresk and Severson 1989, Wrage 1994).

Fruits, especially acorn mast, are important in fall foods of white-tailed deer throughout North America. However, mast has not been identified as important in fall or winter diets in the Black Hills (Hill and Harris 1943, Hill 1946, Schneeweis et al. 1972, Schenck et al. 1972, Richardson and Petersen 1974). Its scarcity in food habit studies may be due to difficulties in identifying mast in rumen or fecal samples (Johnson et al. 1983) and erratic production in this area. Bur oak mast in the Black Hills is 86% digestible and contains 8% crude protein and 8% crude fat (Severson and Kranz 1978) and is likely readily consumed by deer when available.

Forage Production

Extent of the tree overstory is one of the most significant factors affecting production of quality deer forages in forest ecosystems. Considerable information exists on the relationships between forest overstory parameters and understory production. Most of these studies have documented increases in understory as the overstory is reduced (Ffolliott and Clary 1982). Uresk and Severson (1989) developed models that predict understory (by forage class—grasses, forbs, shrubs, and total forage) response in the Black Hills Experimental Forest to basal area of ponderosa pine, in both sapling and pole-sized stands. Grasses and forbs were most abundant in clearcuts and under lower pine basal areas 20 to 60 ft²/ acre (5 to 14 m²/ha); shrub production was quite uniform except in unthinned stands where it was lower. Total annual production varied, over years and stands, from 891 to 2186 lbs/acre (998 to 2450 kg/ha) on clearcuts to 37 to 307 lbs/acre (41 to 344 kg/ha) in unthinned stands.

Equally important, especially for selective feeders such as white-tailed deer, the number of species in the understory increased significantly when the pine overstory was reduced. Uresk and Severson (1989) found 12 and 23 species in the respective understories of unthinned pole and sapling stands. This increased to 22 and 28 species, respectively, when basal area was reduced to 60 ft²/acre (14 m²/ha) and to 40 and 43 species when the overstory was completely removed. Responses of individual species within each forage class are given in Uresk and Severson (in press).

The above data were collected on soils derived from metamorphic parent material. While no information is available for limestone-derived soils, Bennett et al. (1987) indicated most variability in understory production was caused by overstory, precipitation, and position on slope; differences resulting from kind of parent material were minimal.

The understory in aspen stands is an important component of white-tailed deer summer habitat in the Hills (Schneeweis et al. 1972). Although understory increases as aspen overstory is reduced, the response could not be predicted (Severson and Kranz 1976). As conifers invade aspen, however, the understory declines in a predictable manner to increasing basal area or cover of pine as described previously. This has been indirectly verified in two Black Hills studies. Kranz and Linder (1973) reported that understory production in pine, aspen, and aspen-pine stands in the Black Hills declined as pine overstory increased. The greatest production (589 lbs/acre; 660 kg/ha air-dried forage) was in aspen stands, intermediate production (415 lbs/acre; 465 kg/ha) occurred in mixed aspen-pine stands, and the lowest production (215 lbs/acre; 241 kg/ha) was in pure pine stands. Other studies (Severson 1982, Uresk and Severson 1989) have found that only ponderosa pine clearcuts produced as much total forage as unthinned aspen stands. Also, forbs produced under aspen were generally those preferred by deer whereas those in pine clearcuts were less preferred; e.g., yarrow (Uresk and Severson, in press).

Forage production was measured in three of the nine aspen groups identified by Severson and Thilenius (1976). Production in the first group ranged from 714 to 792 lbs/acre (800 to 887 kg/ha). This group contained numerous, small aspen and no conifers. The second group, with fewer aspen, but with significant conifer invasion, produced from 603 to 659 lbs/acre (676 to 738 kg/ha). The third group was the most productive with forage production ranging from 831 to 1094 lbs/acre (931 to 1226 kg/ha). It had aspen densities intermediate to the other types, was characterized by no conifer invasion, and occupied the most mesic sites (Severson 1982).

Little information is available on forage production in other Black Hills habitats, although some studies have

provided cover values that are related to production (e.g., Hoffman and Alexander 1987). In bur oak stringer woodlands in the foothills, total "fine fuel" production (plants < 0.12 in. (3 mm) diameter; oven-dried) ranged from 372 to 966 lbs/acre (332 to 862 kg/ha) (Sieg 1991). Forage production varied on the two main grassland types in the Black Hills. Kentucky bluegrass meadows produced from 652 to 2545 lbs/acre (731 to 2853 kg/ha) (air-dried basis), depending on soil type; whereas drier, mixed prairie produced from 439 to 1436 lbs/acre (492 to 1610 kg/ha) (air-dried basis) again depending on soil type (Pase and Thilenius 1968).

Cover

Biologists agree that cover is an essential component of white-tailed deer habitat, but definitions are disputed and techniques perhaps too broadly applied. Thomas et al. (1979b) combined knowledge from scientific literature with qualitative assessments to develop quantitative cover recommendations for deer and elk in the Blue Mountains of western Oregon based on vegetation characteristics. They established that of the total land base, 40% should be maintained as cover and the remaining 60% as foraging area. They further recommended that two basic cover types be maintained:

- Hiding cover (which provides security) is vegetation capable of hiding 90% of a standing adult deer (or elk) from view of a human at a distance equal to or less than 200 ft (60 m).

- Thermal cover (which provides protection from weather) for deer is 2-5 acre (0.8-2 ha) patches with a minimum width of 300 ft (92.5 m); evergreen or deciduous saplings or shrubs should be at least 5 ft (1.5 m) tall with a 75% or greater canopy cover.

Specialized cover types, such as for fawning, were also identified.

Thomas et al. (1979b) predicated these recommendations with two precautions:

1. They were applicable only in the Blue Mountains and should not be used elsewhere without modification, and

2. They emphasized summer ranges.

The authors pointed out that general recommendations intended to apply to all winter ranges could not be developed because the consequences of errors would be magnified—each winter range is different and must be considered separately before decisions are made on cover alterations. Despite these precautions, application has been perhaps too liberal. As Urness (1989) pointed out, "Although these authors emphasized the prelimi-

nary nature of their guidelines, managers have tended to proceed on the assumption that the relationships are generally applicable. ..." Therefore, managers should carefully examine effects of these recommendations relative to local conditions.

Other structural features of the environment can contribute to cover or influence the way cervids use vegetation for both hiding and thermal cover. While the definitions of Thomas et al. (1979b) centered on vegetation, they used different "land types" as their management foundation on which to predict effects of timber harvest on deer and elk. Other features, such as topography, were used to identify these "land types." They further discussed impacts that topography had on cervid cover recommendations. However, no method has yet been developed to quantify the contribution of topography to cover requirements (Boyd et al. 1986).

White-tailed deer have adapted a "hiding" strategy for avoiding predation; that is, they rely more on dense vegetation cover for concealment (Boyd et al. 1986). However, topography is important on winter range in providing thermal cover. Vegetation of western mountain winter ranges is often split on ridgelines. Northerly exposed slopes are characterized by heavy timber with sparse understories and deep snows while south facing slopes have fewer trees and less snow, but more available food for wintering ungulates (Urness 1989). The low winter sun angle results in higher insolation on south exposed slopes. This not only results in periodic snow melt which makes forage more available, but deer will commonly rest here during the day. Shrubs can provide an intermediate form of thermal cover in these more open habitats by providing protection from the wind (Urness 1989).

Verme (1965) found that white-tailed deer in Michigan consistently chose sites (yards) that effectively moderated adverse weather in preference to those having abundant forage. White-tailed deer in the Black Hills do not exhibit classical yarding behavior but are more scattered over their winter range. However, Kennedy (1992) observed that wintering white-tailed deer in the northern Black Hills did not move far from bed or loaf sites to feed. The value of thermal cover on winter ranges—especially at night, during storms, and on cold, cloudy days—is evident although not well quantified. Shelter-seeking behavior by white-tailed deer takes precedence over selection of other habitat components, including adequate foraging sites, as an energy conservation measure during winter (Verme 1965, Ozoga and Gysel 1972, Nudds 1980, Dusek 1987, and others). In other areas, deer tend to become less selective as forage supplies become limited (Nudds 1980).

Few quantitative data on white-tailed deer use of coniferous overstories for thermal cover during winter are available. Characteristics of both day and night winter bedding sites were quantified in an Ontario study, however. Armstrong et al. (1983) found that bedding sites used at night were among coniferous trees with an overstory canopy that averaged 85%, had a live crown that was 8.2 ft (2.5 m) above the bed site, and were located on north-facing, upper slopes. Many of the night bedding sites were used repeatedly throughout the winter. Conversely, day bed sites were under deciduous trees with a canopy cover of 13% on upper south- or west-facing slopes. Greater snow depth in day-bed areas was attributed to lack of overhead cover. Sites selected at night were those that minimized wind flow, radiant heat loss, and thermal spread; day sites served to increase insolation.

Kennedy (1992) described bedding and feeding sites for adult female white-tailed deer in the northern Black Hills. Daytime winter (1 January-30 April) bedding sites were surrounded by dense, mature ponderosa pine trees (over 9 in [23 cm] dbh), numerous tall shrubs, and under a relatively dense canopy (over 71%). Feeding sites, which included agricultural lands, were more open habitats with an average canopy cover of 23%. Kennedy (1992), whose observations were restricted to daylight hours, did not notice differences in use of slope position or aspect between feeding and loafing sites. Both winter activities were centered on mid-slopes with south-facing aspects.

Kennedy (1992) also characterized spring and early summer (1 May-30 June) habitat use by female white-tailed deer. The deer used immature (5-9 in; 12.7-22.8 cm dbh) and mature (>9 in; > 22.8 cm dbh) aspen stands for loafing during this period. These stands had a generally light overstory canopy (36%), with a dense tall shrub layer, generally beaked hazelnut, that provided both thermal and hiding cover. Adult females fed in more open aspen stands (an overstory canopy cover of 13%), riparian meadows, and clearings.

Stefanich (1995) stated that aspen in the overstory and horizontal screening cover best discriminated deer use sites from random sites during summer in the northwestern Black Hills. Areas with a particular level of horizontal screening cover were selected regardless of cover type. Stefanich (1995) noted that horizontal screening cover averaged 51% in aspen/birch stands generally but was 63% where deer were found. In pine, screening cover averaged 35% but was 45% at sites used by deer.

Stefanich (1995) found that deer use of both meadows and open pine sites increased at night during summer. The degree to which they were used appeared related to their proximity to more densely vegetated diurnal habitats. He also stated that the combination of adequate screening cover and abundant forage was provided by aspen/birch stands.

Habitat utilization studies, whether in the Black Hills or elsewhere, need to be interpreted with caution. Two issues need to be considered. One is that the selection of a habitat unit (i.e., a certain cover type) via utilization-availability studies does not necessarily mean that the unit is required or even preferred by the animal (Johnson 1980, Peek et al. 1982, Boyd et al. 1986). The second issue is illustrated by those cases where a habitat component had been lost (i.e., native meadows or open, low-density ponderosa pine stands) and was absent in the preference analysis. A management decision based on these results would likely overlook this habitat as a required component. Another illustration is that a habitat utilization/availability study conducted in 1874 may not yield the same results compared to one conducted today, since the types and arrangements of habitat units are so different. Techniques have been suggested to alleviate some of these problems (Johnson 1980) but careful interpretation of results is recommended, especially when developing management strategies.

INTERACATIONS WITH OTHER UNGULATES

Cattle

Deer and cattle can compete for food and cover. Cattle in the Black Hills consumed mostly grasses (54-69%), followed by shrubs (20-28%) and forbs (Uresk and Lowrey 1984, Uresk and Paintner 1985). Deer consumed little grass during summer but ate increasing amounts during fall and those winters when snow depth did not preclude its availability (Schneeweis et al. 1972, Schenck et al. 1972). Forbs were important to both cattle and deer.

From preliminary, indirect assessments in the central Black Hills, Hamm (1973) speculated that cattle use of shrubs was minimal. However, subsequent quantitative diet analyses in the Black Hills revealed that cattle used shrubs, such as bur oak, snowberry, and Oregon grape, significantly in late summer and fall. Shrubs constituted up to 31% and 37% of cattle diets in September and October (Uresk and Lowrey 1984, Uresk and Paintner 1985). Shrubs as a group, and these species in particular, are important to deer in winter (Schneeweis et al. 1972, Schenck et al. 1972).

Cattle concentrate in riparian and riparian-like areas; overuse may eliminate shrub and tree regeneration, enhance the establishment of sod-forming grasses such as Kentucky bluegrass, and reduce infiltration (see Skovlin 1984:1018-1026). Heavily compacted Kentucky bluegrass meadows in the Black Hills required up to four years to recover in terms of reduced bulk densities

and increased macropore volumes (Orr 1960, 1975). Such compaction, in combination with a lower water table, along with the competitive influence of the Kentucky bluegrass sod, could impede reestablishment of willows and other woody plants.

Although quantitative data directly applicable to white-tailed deer are lacking, studies have documented the influence of cattle on mule deer habitat quality and behavioral patterns. Moderate (from 0.26 to 0.31 AUM/acre; 0.65 to 0.76 AUM/ha) and heavy (from 0.40 to 0.69 AUM/acre; 0.99 to 1.70 AUM/ha) grazing by cattle resulted in less hiding cover, especially in aspen stands in California (Loft et al. 1987). Kie et al. (1991), also working in California, found that as cattle reduced the availability of herbaceous forage, mule deer decreased the length of their resting bouts and increased the number (but not the length) of their feeding bouts each day.

Lonner and Mackie (1983) suggested that competition for food may be less important than competition for space and that allocation of area, rather than forage, may be a more ecologically sound strategy for management. Critical areas necessary for the survival of native ungulates generally encompass a relatively small proportion of the total system. This led McLean (1979) to recommend that such areas receive preferential treatment. These recommendations were made for situations where competitive interactions were intense, such as between cattle and elk. There is little quantitative information on social/behavioral interactions between livestock and white-tailed deer.

Mule Deer

White-tailed and mule deer have coexisted in the Black Hills for millennia. Food habit studies for mule deer in the Hills are lacking but it is likely that diets of both species are similar (Richardson and Petersen 1974). Therefore, their continued coexistence is probably based on differences in habitat use. Mule deer tend to occupy more open habitats with rough, rocky topography; white-tailed deer are found in relatively more dense habitats such as pine and aspen stands and riparian areas. As a result, mule deer are relatively more abundant in the southern Black Hills than in the northern. Despite the more open habitat conditions that existed in the Black Hills in 1875, Lt. Col. Dodge reported that "red deer" (white-tailed deer) were more numerous than any other animal but further described "black-tailed deer" (mule deer) as also being numerous (Dodge 1965).

Similarity of food habits and some overlap in habitat use where these species occur together indicate potential competition in local areas (Mackie 1981). In ob-

served interspecific encounters, dominance was divided and apparently based on size. In Arizona, mule deer were much larger than white-tailed deer and were dominant in all interactive instances (Anthony and Smith 1977). The general pattern is for the two species to ignore each other in most encounters (Marchinton and Hirth 1984). Evidence from elsewhere (Wishart 1980) and from the Black Hills (Oceanac 1977) suggests that mule deer and white-tailed deer occasionally hybridize.

Overall, Kramer (1972) concluded that competitive interactions between mule and white-tailed deer are not important because they occupy divergent ecological niches. Even so, the abundance of the two cervid species has changed because of alterations in habitat conditions and differential hunting mortality (Kramer 1972).

Elk

As with mule deer, white-tailed deer have coexisted with elk in the Black Hills since the late Pleistocene; however, the subspecies involved was the Manitoban elk, which was extirpated from the Black Hills by 1888 (Bryant and Maser 1982). Several introductions of Rocky Mountain elk from the Yellowstone region of Wyoming were made into the Black Hills between 1912 and 1914 (Turner 1974).

Elk in the southern Black Hills consume mostly graminoids, followed by forbs, and then browse such as lead plant and mountain mahogany sometimes in the winter (Wydeven and Dahlgren 1983). Overlapping food habits are not normally considered important when assessing interactions between elk and white-tailed deer; elk are normally considered grazers, feeding primarily on grasses while deer consume forbs and shrubs (Nelson 1982). If overpopulation of either species occurs or if both species rely on the same forage group (e.g., shrubs on winter range), serious competition will occur and elk will likely dominate (Nelson 1982). Such competition could develop on common winter range, such as in the northern and northeastern Hills. Elk concentrations could also interfere with key elements of white-tailed deer habitat. For example, elk browsing has limited aspen regeneration (Olmstead 1979, DeByle 1985). Future competitive trends between white-tailed deer and elk will depend on the population levels of the two species and the quality and quantity of habitat available to both.

TECHNIQUES FOR MANAGING HABITATS

The Black Hills biotic complex evolved under the continual influence of disturbances that produced a mosaic of vegetative types. How should we adjust our

forest management practices to operate in concert with natural disturbances to realize a viable functioning ecosystem? One important component of this ecosystem is a healthy and productive white-tailed deer population. The following techniques, if properly applied, would not only create better conditions for deer, but would also help restore and maintain the historically diverse landscape of the Black Hills.

Timber harvest and prescribed burning can be used to create habitat mosaics on deer ranges in the Black Hills. Most standard silvicultural systems for ponderosa pine can be used in the Black Hills; however, the even-aged management techniques preferred for timber production (Boldt and Van Deusen 1974) may be the least preferred system for deer habitat. Boldt and Van Deusen (1974) suggested that the group-selection method would best simulate the natural structural arrangement resulting from fires, bark beetles, and wind. Seed-tree and clearcut methods both enhance growth of understory plants, but they can result in large accumulations of logging slash. Light ground fires can be used to reduce these fuel accumulations, as well as to thin pine seedlings (Boldt and Van Deusen 1974).

Although managers recognize the need for precommercial thinning in ponderosa pine stands, many are reluctant to use prescribed fire in this capacity due to the potential hazards (Wright and Bailey 1982). With increasing emphasis on ecosystem management, the use of timber harvest will be limited to a framework that focuses on maintaining productive, sustainable forests. Although timber cutting can accomplish some of the same objectives as burning, fire is necessary to realize some benefits that cannot be achieved by cutting, such as those related to affects on the understory, soil chemistry, microbes, and decomposition rates. Fire differentially affects soil and water properties depending on intensity of the burn, fuel type, soils, climate, and topography (Wright and Bailey 1982). Burning speeds up decomposition rates, releasing nutrients to the environment within minutes or days, instead of years or decades. Therefore, timber harvest and prescribed burning are not ecologically equivalent. Structurally similar habitats may result from cutting or burning, but system dynamics will be different.

The forage producing capability of a forested stand can be improved by manipulating the overstory. Reduction or removal of this overstory can increase forage as discussed in the section on Forage Production. The rate of understory response will depend on the treatment (fire and/or harvest), number of remnant plants or propagules, site capability, and weather patterns following overstory removal. Cleared pine stands may revert back to conifers directly or go through a series of seral stages, such as those dominated by aspen or bur oak. These seral stages, in addition to other community

types, provide additional forage that is composed of different species from those found under dense pine canopies. All of these situations, collectively, provide a diverse and productive forage base for deer and other herbivores.

However, silvicultural practices that increase forage may not provide adequate cover (Stefanich 1995). It is extremely important that the proper arrangement of forage and cover areas be maintained. Management strategies directed toward providing an optimum forage source close to cover reduce energy expenditures for travel and searching for food. Managers of deer habitat in the Black Hills can use this approach because of irregular topography and the pronounced north slope-south slope effect. Such strategies will, however, require unique and site specific arrangements of cover and foraging areas.

From an economical and ecological standpoint, fire is the best tool for reducing pine seedling encroachment into forest openings and meadows. Gartner and Thompson (1972) used spring burning to eliminate ponderosa pine seedlings in foothills grasslands. They found headfires (fires that burn with the wind) most effective in killing young pine seedlings.

Proper livestock management is critical to minimizing conflicts with white-tailed deer and to ensure that enough fine fuels (mainly grasses) are present to carry prescribed fires. Critical deer ranges and some riparian zones may require protection from cattle grazing, at least during late summer and fall. Recently planted or burned areas may need to be protected for one or more growing seasons. On those areas traditionally grazed, cattle grazing may need to be deferred for at least one growing season before prescribed burning to allow the accumulation of adequate fine fuels. In the absence of adequate fine fuel loads, fireline intensities can be reduced severely and burning will be patchy. The result of burning with inadequate fine fuels can be incomplete combustion of heavy fuels and poor shrub regeneration.

However, properly managed cattle grazing may improve deer habitat. Severson and Urness (1994) offered four ways that livestock grazing can improve wildlife habitats—three of which may be applicable in the Black Hills:

1. Altering composition of the forage base,

2. Increasing productivity of selected forages, and

3. Increasing the nutritive quality of forages by removing decadent material and setting back the phenology of the plants.

Although none of these techniques have been proven effective in the Black Hills, evidence from other regions (e.g., Urness 1990) suggests that livestock grazing shows some potential in accomplishing these objectives.

Other strategies for improving the quality of white-tailed deer habitat in the Black Hills include hand-cutting shrubs, seeding, and planting. Shrubs such as aspen, paper birch, beaked hazel, and red osier were hand cut in Minnesota to increase deer browse (Erickson et al. 1961). Bulldozing and cut-a-way disks expose mineral soil and open the area to sunlight to encourage seedling establishment of shrubs. Dietz et al. (1980) tested a variety of shrub species for replanting depleted big game range in the Black Hills.

Riparian stands often constitute an important part of winter habitat for white-tailed deer (Peek 1984). Rejuvenating degraded riparian stands may be a multi-faceted process requiring watershed level treatments. For example, silvicultural treatments that reduce the density of pine trees and increase stream flows (e.g., Anderson 1980) enhance the survival of water-limited plants. In addition, cottonwood and willow poles can be hand planted along streamsides; in Arizona, this technique was an inexpensive method for reestablishing these species (Swenson and Mullins 1985). Reintroducing beavers in some areas can raise the water table, enhance water quality, and protect streams from large-scale scouring (Parker 1986).

MANAGEMENT RECOMMENDATIONS

This paper has emphasized the habitats of white-tailed deer. It created a foundation of information that managers can use to incorporate habitat recommendations for white-tailed deer into ecosystem level planning. Public land managers must now realize, as advocated by Patton (1993), that management for any single species must include the effects of this management on other species within the ecosystem. Management of Black Hills ecosystems is becoming more complex. The process of integrating wildlife habitat requirements into a yet undefined ecosystem framework offers significant challenges by itself; the process of incorporating the needs of other forest users into this design may appear staggering. This integration will necessitate the introduction of new techniques and approaches, and the application of the principles of landscape ecology (Morrison et al. 1992), into the decision making process.

Successful integration of the habitat needs of the white-tailed deer into an ecosystem framework will also involve cooperative efforts among managers. The formation of a group of resource specialists charged with integrating information on an ecosystem level will be necessary (e.g., Thomas et al. 1976, 1979a). The overall task of such a group would consider more than just deer, but a first "subtask" relating to deer would be to examine the distribution of critical habitat in the

absence of land ownership constraints. The second would be to identify high priority land to be managed to provide missing components on winter, transition, and summer ranges. At this point, it might also be necessary to identify lands that should be purchased or entered into long-term leases to maintain as deer habitat. Finally, this group would focus on watershed level questions of the amount and distribution of forage and cover. Ultimately, this information can then be combined with research results and information on other species to develop a model to predict the effects of forest alterations on various wildlife species.

Pending the development of an integrated landscape approach to ecosystem management, we offer the following recommendations for enhancing habitats for white-tailed deer in the Black Hills.

Winter Range

A significant proportion of white-tailed deer in the Black Hills migrate to lower elevations during winter (Richardson and Petersen 1974). Winter ranges are currently the most critical areas requiring management emphasis. Winter weather influences deer condition and mortality because of increasing snow depths and cold temperatures. Movements and feeding patterns are controlled by snow depth and condition (Kufeld et al. 1988). Although deer can forage through limited soft snow, increasing depth and/or crusting impedes foraging for low growing vegetation such as bearberry or Oregon grape (see review by Severson and Medina 1983:17). Severe winters are sometimes responsible for high deer mortality in the Black Hills (Petersen 1984).

This prompts a question regarding management of winter ranges: Should winter habitats be designed for the occasional severe winter or should they be designed for the mild to average winter? Application of the former would create a more stable population over time, but costs would be higher. While endorsement of the latter would be less costly, occasional severe deer losses would have to be expected and accepted. Also, periodic heavy losses of deer would give woody forage species a chance to recover (Urness 1990).

Several actions can enhance white-tailed deer winter range in the Black Hills. First, key winter ranges, or those that are particularly critical and support a large number of deer, need to be identified, assessed, and prioritized for treatment. On these ranges, stringent actions such as implementing grazing systems that remove livestock before they start to utilize woody vegetation are warranted. Grazing systems that defer or exclude livestock before they start consuming shrubs (about midsummer; Uresk and Lowrey 1984, Uresk and Paintner 1985) allow regrowth of herbaceous vegetation,

upon which deer also depend. Further, if an adequate woody forage base is not present, seeding and/or replanting might be required (Dietz et al. 1980). Human activities may also have to be minimized on these key ranges.

The next goal that must be met to enhance winter range is to increase the availability of protein and energy (Dietz 1972). Given that south-facing slopes are more likely to be snow-free in the winter, these slopes should be managed to maximize forage production. South-facing slopes and riparian zones are areas where white-tailed deer in other regions concentrate in the winter (Payne and Bryant 1994). Forage production can be maximized by removing all pine trees with the exception of isolated larger trees with wide canopies. The remaining understory should be prescribed burned to stimulate shrub growth and to temporarily increase nutrient availability, particularly protein. Forage on north slopes may be nearly inaccessible in deep snow. However, north slopes can provide excellent cover, and forage can be provided in patch cuttings.

Both burning and timber harvest can be used to reduce the overstory, and hence, increase the quantity of forage. However, burning can be used to increase the quality of forage, as well, by removing decadent material and setting back the phenology of the plants. Overstory harvest, in itself, does not enhance understory forage quality (Severson and Uresk 1988). Most deciduous browse species sprout following burning, and these young succulent sprouts are usually more nutritious than unburned mature plants. Although such increases in nutrient content of shrubs following burns have been documented, for example by DeByle et al. 1989 in Idaho, Taber and Dasmann (1958) in California, Lay (1957) in the southeast, and Stransky and Halls (1978) in east Texas, these increases do not last for more than one to three years (Taber and Dasmann 1958; Asherin 1973).

On areas where fires have been suppressed for long periods, burning when plants are dormant is preferable to reduce fire intensity. However, fire intensity is a critical factor in stimulating shrub sprouting. In contrast to cool spring and fall prescribed burns, Bock and Bock (1984) noted that an autumn fire that became a crown fire killed pines of all sizes and, as a result, most shrub species increased dramatically. Since the benefits of increased forage quality resulting from fire are ephemeral, at least 10% of the area should be treated each year to maintain some portion of the forage base in a vegetative state (Payne and Bryant 1994).

In addition, enough small areas should be treated at one time to disperse browsing impacts (Wright and Bailey 1982). The increased nutritive content, succulence of the new shoots (Asherin 1973), and the availability of

young sprouts from a variety of shrub species (Short et al. 1977; Regelin and Wallmo 1978) tend to attract grazing and browsing ungulates to newly burned areas and there is some danger that impacts resulting from these concentrations could damage the new growth. Most cervids, including white-tailed deer, tend to use burned areas long after the nutrient flush has declined but not as heavily. The long-term attractiveness of burned areas may be attributed to increased habitat diversity or edge, increased production of preferred forage, and/or increased forage diversity (see Severson and Medina 1983:42).

Riparian areas on winter ranges are valued because they provide both food and cover. Many of the techniques discussed above also apply to riparian areas. Further, removal of a significant portion of trees on the uplands may enhance stream flows (Anderson 1980), which in turn provides better moisture conditions for the growth of deciduous trees and shrubs. Introduction of beavers to raise the water table may also enhance streamsides for woody plant growth (Parker 1986). Since livestock utilization of shrubs increases dramatically later in the summer (Uresk and Lowrey 1984, Uresk and Paintner 1985), removal of cattle from riparian areas before grasses cure will reduce their impact on woody plants.

Prescribed burning shows some promise for stimulating decadent bur oak stands and at least temporarily setting back Kentucky bluegrass along streams (Sieg in press). A combination of adequate fine fuels and relatively dry conditions is critical to achieve intensities necessary to stimulate shrub sprouting. To meet minimum fine fuel requirements, herbivore utilization levels must be kept low enough to allow accumulation of a minimum of 784 lbs/acre (700 kg/ha). Sieg (in press) also concluded that fall burns are more likely to provide the conditions necessary for complete combustion, and emphasized the importance of wind speeds in excess of 8 mi/hr (13 km/hr).

Seeding and planting may be appropriate methods for reestablishing depleted winter ranges on uplands also but are generally economically feasible only on key winter ranges. Dietz et al. (1980) tested reestablishment of both native and introduced shrubs, including chokecherry, pin-cherry, common juniper, mountain mahogany, Saskatoon serviceberry, inland ceanothus, bitterbrush, buffaloberry, and silverberry. Mountain mahogany and bitterbrush grew better than other species by direct seeding in the fall. Chokecherry established by planting nursery stock in the spring did better than those plants established by seeding or planting potted plants. Silverberry and silver buffaloberry grew best of the bare-root nursery stock. Saskatoon serviceberry, common juniper, and inland

ceanothus had poor success, regardless of the technique. Protection of new shrub plantings may be necessary since deer and other herbivores may destroy plants before they are successfully established.

Adequate cover is so critical on winter ranges that Thomas et al. (1979b) suggested that separate prescriptions be developed for each winter range. Some principles do apply, however. First, as discussed in the section on Cover, shelter-seeking behavior by white-tailed deer takes precedent over selection of other habitats, including those used for feeding. This was partially documented for white-tailed deer in the Black Hills by Kennedy (1992), who noted that deer did not move far from bedding sites to feeding sites. This demonstrates the importance of locating cover areas close to foraging areas. Since south-facing slopes are primary feeding sites on winter ranges, efforts to develop cover should be directed to the upper portions of north facing slopes, which were used as night bedding sites in Ontario (Armstrong et al. 1983). These sites should support dense, coniferous trees with an overstory canopy of 85% and with a live crown that is 8.2 ft (2.5 m) above the ground (Armstrong et al. 1983). Further, sites on south-facing slopes such as first order drainages could be maintained as cover areas. Such areas should contain mature coniferous trees (over 9 in [23 cm] dbh), with a relatively dense canopy (over 71%), and numerous tall shrubs that Kennedy (1992) recommended for daytime bedding sites.

Transitional Ranges

A period more critical than mid- or late winter may be the winter-spring transition. Debilitation and death have commonly occurred during this period in the upper midwest (Verme and Ozoga 1971). Suggested reasons for these winter-spring transition deaths are that the animals' metabolic rates have increased, perhaps in response to increasing photoperiod; and especially for pregnant does, their energy demands have also increased. Their metabolic systems are not able to respond to a sudden external trauma, such as a late spring blizzard (Verme and Ullrey 1984).

Such conditions occasionally occur in the Black Hills. During spring, as snowmelt clears meadows dominated by Kentucky bluegrass, deer switch diets from ponderosa pine needles and low quality browse to bluegrass and clovers, which initiate growth early. The water content of the new green forage is so high deer cannot consume enough material to meet energy demands (Dietz and Nagy 1976). Sudden dietary changes can result in scours, impairment of rumen function due to a delayed microorganism response, and secondary infections in the digestive tract (Dietz and Nagy 1976).

The negative impacts of these sudden dietary shifts could be mitigated if a higher quality forb/tall shrub forage base was present, both on winter and spring transitional ranges.

As mentioned earlier, in spite of the importance of a viable forage base on fall transitional ranges, many species identified in deer food habit studies in the Black Hills have significant nutritional limitations, or their low growth form limits their availability. Fall forage availability and quality may be increased in two ways:

1. Where bur oak and aspen dominate, these stands should be cut and/or burned to stimulate sprouting;

2. On fall ranges with mostly pine, pine stands should be opened up to stimulate the growth of tall nutritious shrubs.

Follow-up prescribed burning and/or planting may be necessary to maximize availability of nutritious shrubs.

Bur oak is a key species contributing to the fall forage base in the northern and eastern Black Hills. Bur oak is a vigorous sprouter (Johnson 1990) that produces browse and some mast. Prescribed burning shows some promise for rejuvenating decadent bur oak stands. On the eastern flanks of the Black Hills, burns conducted in the spring before deciduous trees leafed out increased numbers of sprouts on bur oak, green ash, and box elder in riparian-like stands (Sieg 1991). Bur oak buds and twigs are not nutritionally adequate to sustain white-tailed deer, but their quality may be improved by burning, which produces young sprouts, removes decadent material and sets back the phenological stage of the plants. Sprouts of gambel oak from burned stands contained greater crude protein and phosphorus and were more digestible than those of unburned stands in Colorado (Pendleton et al. 1992). Post-fire bud tissue had the highest nutrient content, with a mean of 9.5% crude protein, 0.19% phosphorus, and 34% in vitro digestibility, compared to 6.5% crude protein, 0.12% phosphorus, and 26% digestibility for unburned bud tissue.

Acorn mast is nutritionally adequate (Severson and Kranz 1978), however, and consumption of mast allows deer to build up fat reserves for the winter (Pekins and Mautz 1987, 1988). Acorn crops are inconsistently produced in the Black Hills. Severson and Kranz (1978) recommended selectively cutting bur oak stands, whereby the best acorn producing trees are left, and smaller, less vigorous oaks are removed to encourage sprouting. Similar recommendations were made for gambel oak (Payne and Bryant 1994). Selective removal of bur oak trees for fuelwood would also encourage re-establishment of associated shrub species. Further, in mixed oak-pine stands, selective removal of pine trees may enhance reproduction of oak and associated shrubs.

The production of some tall, relatively nutritious shrubs and saplings (e.g., chokecherry, serviceberry, and aspen) can be enhanced on some sites on fall ranges by significantly reducing the pine overstory and stimulating the understory. Removing competing pine and clearcutting aspen results in the greatest response of aspen suckers (Schier et al. 1985). However, harvest of pines, in itself, has been only sporadically successful for stimulating chokecherry and serviceberry in the Black Hills (Uresk and Severson 1989). Prescribed burning can be used to stimulate sprouting since chokecherry, serviceberry, and aspen are prolific root or crown sprouters (Wright and Bailey 1982). If remnants of these species are present in the understory, they will respond favorably to especially intense fires (Bock and Bock 1984). In the absence of tall shrub remnants in the understory, seeding and/or planting may be warranted.

Summer Range

As previously discussed, summer ranges receive less attention because forage condition and availability generally exceed that on winter ranges. Further, poor-condition summer range is reflected in lower deer productivity and the effects are often insidious rather than dramatic.

Maintaining and enhancing hardwood communities should be a major element in habitat management in the Black Hills (Stefanich 1995). Aspen stands provide both cover and forage on summer ranges (Kennedy 1992). Some, such as the aspen/beaked hazelnut or aspen/ironwood types, provide better cover than forage; others, such as the aspen/western wild rose/Kentucky bluegrass/clover type (Severson and Thelinius 1976), provide better forage than cover.

Total removal of the overstory by clearcutting or stand-replacing fires has a vital role in management of deer summer ranges. That role is to remove pine, spruce, or mature aspen overstory to allow seral aspen stands to develop on those sites where remnant aspen in the form of trees or root suckers occur. As Severson (1982) suggested, a variety of seral aspen stages should be a goal in order to maximize cover and forage diversity. Aspen cutting programs in the Black Hills are impeded by the lack of a commercial market for aspen, which is related to the limited occurrence of aspen in this area. Cutting aspen for fuelwood, however, may be a viable option. Certain aspen stands may not respond to clearcutting, however (Patton and Jones 1977). The age of the stand can influence its ability to resprout (see Severson and Medina 1983:37-39). Such stands may require burning to induce adequate sprouting.

Prescribed burning can be a useful technique for regenerating aspen stands and removing small compet-

ing conifers, and may be necessary for renovation of decadent stands (Patton and Jones 1977). Increased root temperature caused by exposure of soil to sunlight is the cardinal factor in stimulation of suckering (Maini and Horton 1966, Steneker 1974). Apparently, in younger, vigorous aspen stands, the increased soil temperature resulting from clearcutting is adequate stimulation, although light burning to create a blackened, heat absorbing surface will help (Shirley 1932).

As aspen stands pass maturity, a more drastic treatment, which would include higher intensity fires, may be necessary to induce adequate suckering to replace the parent stand. Litter and duff under older stands are likely deeper, and since litter is an excellent insulator, it can prevent adequate soil warming if only the overstory is removed. A moderate to high intensity burn creates higher soil temperatures three ways: by heating the mineral soil, by removing all insulating effects of litter, and by creating a heat-absorbing blackened surface (Severson and Medina 1983:38). It is difficult, if not impossible, to prevent root suckering by intense burning (Horton and Hopkins 1965, Schier and Campbell 1978).

Although the need for hot burns to regenerate aspen is not fully understood, there is ample evidence that fire of sufficient severity will kill old trees, cause profuse aspen root suckering, and increase forage production (DeByle 1984) and forage quality (DeByle et al. 1989). Although suckering as a means of aspen regeneration has been emphasized, one study reported that severe burning may also induce aspen seed establishment. In Yellowstone National Park, concentrations of aspen seedlings were found in riparian zones that had been burned down to bare mineral soil following the 1988 wildfires (Kay 1993).

Timing of prescribed burns in aspen stands will also influence the desired outcome. Most managers prefer to burn in the spring or fall due to ease of control, cost effectiveness, and safety. Bartos et al. (1991) noted that spring burns produced a greater number of aspen suckers than fall burns in western Wyoming. However, other preliminary results suggest that summer burns show some promise for removal of encroaching conifers and top killing decadent shrubs (Weaver and Benscoter 1989).

The influence of soil type on the outcome of prescribed burning or cutting on aspen stands has been documented. Clones located on Mollisols (or dark prairie soils) show the greatest potential for responding to prescribed burning; those stands on Alfisols (leached, nutrient-poor soils that are often associated with pine forests in this area) may not respond as vigorously (e.g., Cryer and Murray 1992). The higher success of treatments on Mollisols is likely attributable to the higher nutrient levels associated with these soils.

Ponderosa pine types also can be managed for either cover or forage. As discussed in the section on Forage Production, most forage is produced in stands with a basal area of 40 ft²/acre (9 m²/ha) or lower, but significant quantities of bearberry and yellow vetchling are produced in stands with basal areas of 80 ft²/acre (23 m²/ha) or less (Uresk and Severson 1989). Some degree of security is also provided by stands with 40 to 120 ft²/acre (9 to 28 m²/ha) basal area, depending on size (and therefore density) of the trees in the stand.

Stands with 80 to 120 ft²/acre (23 to 28 m²/ha) basal area provide a little food and some cover; therefore, their value as deer summer range is minimal unless combined with other stands or forest types that provide better food. The production of bearberry and yellow vetchling is a positive contribution, but the absence of a diverse understory and lower overall forage production limits their contribution. These stands can be a part of summer habitats if they are closely associated with aspen stands, dense riparian zones, and/or more open ponderosa pine stands.

More open pine stands with basal areas less than 40 ft²/acre (9 m²/ha) produce more total forage and greater species richness (Uresk and Severson 1989). The value of such stands as white-tailed deer foraging areas vary depending on availability of other kinds of foraging sites and the size of the stand. Prescribed fire could also be used to create phenological diversity that enhances the availability of some nutrients. The nutritional value of non-woody understory vegetation, like shrubs, may increase for one to two years after burning (Pearson et al. 1972).

RESEARCH NEEDS

The white-tailed deer is one of the most studied animals in North America, yet questions remain about this native ungulate in the Black Hills. Much of the available information has been derived in ecosystems that are quite different from the Black Hills and from populations that are non-migratory. The vegetation of the Black Hills has evolved under weather patterns and fire regimes that differ significantly from eastern and northern white-tailed deer habitats. Further, ponderosa pine forests in the Black Hills are unique in their regenerative abilities. Compared to conditions at the turn of the century, vegetative patterns in the Black Hills have changed largely due to the expansion of pine-dominated communities.

The development of a successful white-tailed deer management plan for the Black Hills is impeded by a lack of information in three general areas:

1. How changes in the Black Hills ecosystem have affected white-tailed deer foraging strategies, and how these changes have influenced herd productivity;

2. How changes in the Black Hills vegetative patterns have affected how white-tailed deer use foraging and cover areas; and

3. What ecologically sound, cost effective methods best provide desired micro- and macro-habitat conditions.

How have white-tailed deer foraging strategies changed in response to expanding pine communities? Are deer now consuming plants that they would not have eaten previously because more preferred forage species are scarce or no longer present? Assessment of white-tailed deer use of marginal foods, such as pine needles, during certain seasons would be necessary to determine if this reflects preference or if it indicates an inadequate forage base. Does reliance on marginal foods induce nutritional problems, and if so, what are the effects on deer productivity? Finally, will mitigative measures result in immediate responses? Consequences of nutritional deprivation on deer may be insidious, that is, reflected in production of fawns that have a reduced ability to survive or reproduce. Hence, it may be necessary to examine these effects over several generations.

An improved understanding of deer habitat requirements at both macro- and micro-habitat scales is needed. Have expanding pine communities resulted in the loss of seral communities important to deer for feeding and/or cover? For example, early seral stages of aspen are uncommon in the Black Hills today and habitat use studies conducted under current conditions may overlook the importance of such an uncommon type. How can habitat utilization/availability studies be enhanced to better identify missing or uncommon habitat components and accurately reflect habitat requirements at both the macro- and micro-habitat levels? What is the optimum size of a stand or an opening, and does this vary depending on seasonal use and site characteristics?

Even if accurate habitat use patterns can be determined, how should macro-habitats be arranged both in space and time? Is the juxtapositioning of various habitat components more important than the actual size of the components? We have referred to work from other areas regarding the forage and cover ratios (i.e., Thomas et al. 1979b, for elk and mule deer), but are these ratios applicable in the Black Hills? Further, what is the role of topography in providing cover? How do interspersed agricultural lands and key habitats, such as riparian areas, influence deer use of habitats?

The last problem area focuses on identifying techniques to alter vegetative structure and composition to provide and maintain adequate deer habitat. Prescribed burning is a tool worth investigating to alter vegetative structure in the Black Hills, because fire was a significant force in developing these communities. The role of fire in maintaining interspersion and diversity of seral stages is generally understood, but the importance of fire in maintaining phenological and nutritional diversity that leads to greater availability of some nutrients is more subtle and perhaps more complex. Research is needed to assess whether prescribed burning can be used to improve forage quality for white-tailed deer. Further, information on integrating timber harvest and prescribed burning to meet cover and forage needs is necessary. Finally, questions remain as to how natural fire regimes, including mid-summer burns, can be reinstituted without severe conflicts with expanding human populations.

These information gaps need to be addressed in an ecosystem framework. Researchers and managers need to jointly work toward identifying how Black Hills systems function, the role of disturbances in their maintenance, and how to best achieve structurally and functionally diverse systems. This understanding will provide the best chance of providing habitat not only for white-tailed deer, but also for a multitude of other animal and plant species.

ACKNOWLEDGMENTS

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APPENDICIES 1 AND 2 FOLLOW

APPENDIX 1

Common and scientific names of plants used in this publication.

Nomenclature follows Great Plains Flora Association (1986).

Common name	Scientific name	Common name	Scientific name
Graminoids		**Shrubs and trees (cont'd)**	
western wheatgrass	*Agropyron smithii*	beaked hazelnut	*Corylus cornuta*
big bluestem	*Andropogon gerardii*	silverberry	*Eleagnus commutata*
little bluestem	*Andropogon scoparius*	green ash	*Fraxinus pennsylvanica*
sideoats grama	*Bouteloua curtipendula*	common juniper	*Juniperus communis*
blue grama	*Bouteloua gracilis*	Rocky Mountain juniper	*Juniperus scopulorum*
buffalograss	*Buchloe dactyloides*	ironwood	*Ostrya virginiana*
sun sedge	*Carex heliophila*	ninebark	*Physocarpus monogynus*
Junegrass	*Koeleria pyramidata*	Black Hills spruce	*Picea glauca*
Kentucky bluegrass	*Poa pratensis*	ponderosa pine	*Pinus ponderosa*
needle-and-thread	*Stipa comata*	cottonwood	*Populus* spp.
green needlegrass	*Stipa viridula*	quaking aspen	*Populus tremuloides*
Forbs		pin-cherry	*Prunus pensylvanica*
yarrow	*Achillea millefolium*	chokecherry	*Prunus virginiana*
yellow vetchling	*Lathyrus ochroleucus*	bitterbrush	*Purshia tridentata*
twinflower	*Linnaea borealis*	gambel oak	*Quercus gambelii*
alfalfa	*Medicago sativa*	bur oak	*Quercus macrocarpa*
common dandelion	*Taraxacum officinale*	fragrant sumac	*Rhus aromatica*
white clover	*Trifolium repens*	currant	*Ribes* spp.
Shrubs and trees		western wild rose	*Rosa woodsii*
		beaked willow	*Salix bebbiana*
boxelder	*Acer negundo*	sandbar willow	*Salix exigua*
Saskatoon serviceberry	*Amelanchier alnifolia*	yellow willow	*Salix lutea*
bearberry	*Arctostaphylos uva-ursi*	buffaloberry	*Shepherdia argentea*
lead plant	*Amorpha caneseens*	wild spiraea	*Spiraea betulifolia*
fringed sagebrush	*Artemisia frigida*	white coralberry	*Symphoricarpos albus*
Oregon grape	*Berberis repens*	western snowberry	*Symphoricarpos occidentalis*
water birch	*Betula occidentalis*	American elm	*Ulmus americana*
paper birch	*Betula papyrifera*	grouseberry	*Vaccinium scoparium*
inland Ceanothus	*Ceanothus herbaceous*	**Other**	
hackberry	*Celtis occidentalis*	lichen	*Usnea* spp.
mountain mahogany	*Cercocarpus montanus*		
red osier	*Cornus stolonifera*		

APPENDIX 2

Common and scientific names of animals and insects used in this publication.

Common name	Scientific name
beaver	*Castor canadensis*
elk	*Cervus elaphus*
Rocky Mountain elk	*Cervus elaphus canadensis*
Manitoban elk	*Cervus elaphus manitobensis*
mountain pine beetle	*Dendroctonus ponderosae*
mule deer	*Odocoileus hemionus*
white-tailed deer	*Odocoileus virginianus*

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